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Evolution of displays within the pair bond

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Although sexual selection is an important cause of display evolution, in socially monogamous species (e.g. many birds), displays continue after formation of the pair bond. Here, we consider that these displays evolve because they stimulate the partner to increase investment in offspring. Our study is motivated by elaborate mutual displays in species that are largely monomorphic and have long-term pair bonds (e.g. the great crested grebe, *Podiceps cristatus*) and by many empirical results evidencing that display manipulation affects parental investment. Using population genetic models, we show that a necessary condition for the permanent establishment of mutual displays in the pair bond is that the benefit of investment by the pair is more than twice that resulting from investment by a single individual. Pre-existing biases to respond to displays by increased investment are a necessary component of display evolution. We also consider examples where one sex (e.g. males) stimulates increased investment in offspring by the other sex. Here, display and additional investment cannot evolve permanently, but can increase and linger at high frequency for a long time before loss. We discuss how such transient effects may lead to the evolution of permanent displays as a result of evolution at additional loci.

1. Introduction

In socially monogamous species, pair bonds persist through a breeding season and sometimes for life [1,2]. Social monogamy is particularly common in birds [3], which are well known for their elaborate socially selected traits, often attributed to sexual selection. However, some of the most striking displays involve bird species that form long-term pair bonds, with apparently limited opportunities for sexual selection [4–6]. For example, in the great crested grebe, both the male and female gain showy plumages in the breeding season and use them in elaborate mutual displays (figure 1*a*), which continue long after pair formation [4]. Although social monogamy reduces opportunities for sexual selection, it creates an environment in which one partner can stimulate the other to invest in offspring (including into eggs, resource defence and the rearing of young). Many experimental manipulations of traits of one partner in the pair, including his or her plumage ornaments, coloration and vocalizations, have been shown to alter investment by the other partner, with increased exaggeration of the display typically increasing investment (figure 1; [8–10,13–16]).

Here, we consider conditions for social displays to evolve when their prime effect is to stimulate the partner to invest more in his or her brood. We build population genetic models to show how, in the complete absence of sexual selection, mutual displays and associated showy traits permanently evolve in pair-bonding species. The main necessary conditions are twofold. First, fitness benefits from increased investment by the pair must act synergistically, i.e. benefits must be more than twice that expected from a single partner's investment, to an extent that depends on other factors, such as the costs of the display. Second, the response alleles must be present due to a pre-existing bias, which is not expressed until triggered by the display.

Investment in response to the other sex is not confined to species with mutual displays. Many examples of differential investment have been described, in which

Figure 1. Displays in pair bonds. (*a*) Elaborate displays between a pair of great crested grebes (*Podiceps cristatus*) include the illustrated weed display. Both the male and female gain showy plumage in the spring, and either may initiate a display, which continues long after the pair-bond forms ([4]; figure from Price [7]), drawn by Emiko Paul, reproduced with permission. (*b*) The red spot on the beak of the sexually monomorphic yellow-legged gull (*Larus michahellis*) is the focus of chick solicitation for food. Increasing the size of the red spot increases partner provisioning, irrespective of sex [8]. Photo by Nicole Bouglouan (http://oiseaux-birds.com). (*c*) In the sexually dimorphic zebra finch (*Taeniopygia guttata*), certain colour bands on one sex increase partner provisioning by the other, but the most effective colour differs between the sexes [9]. Photo by Wolfgang Forstmeier. (*d*) In the rock sparrow (*Petronia petronia*), the yellow breast band is present in both sexes, and yellow feathers are found on nestlings. Experimentally, increasing female breast band size results in males defending the nest more aggressively [10]. Other experiments have invoked mate choice and resource competition as contributors to the development of the yellow in both sexes [11,12]. Photo by Christian Kerihuel.

one sex (e.g. the female) paired with the other (e.g. the male) invests more or less in its brood depending on the phenotype of his or her partner [7,9,16]. We extended the symmetric model to show that such asymmetric displays generally evolve only transiently. However, the display can rise to a high frequency before it and the investment response are eventually lost. In the discussion, we consider how evolution at additional loci not incorporated in our models may lead to permanent establishment of the display, rather than its loss.

To isolate effects of investment into offspring, we developed a model in which sexual selection is completely absent, i.e. we assumed random mating and strict social as well as genetic monogamy within each season, with a constant divorce rate across seasons. Parental investment, triggered by a mate's display, increases the number of surviving offspring, thereby encompassing both offspring quality and offspring number. Both display and parental investment lower survival to the following breeding season. Because costs of investment are paid after reproduction, we need to consider age structure. This contrasts with most genetic models of sexual selection, where costs of the male trait are paid either prior to, or during, a single bout of reproduction.

2. Model

Breeding happens once a year. Owing to the complexity of the life history, we assume two-locus haploid genetics. At the locus for the display, B, allele B_1 produces no display, whereas B_2 leads to the production of a costly display. At the investment (or response) locus, A, allele A_1 leads to no increased investment, whereas A_2 causes individuals to increase their investment in offspring in response to a displaying mate. This yields four individual genotypes, A_1B_1, A_1B_2, A_2B_1 and A_2B_2. We track numbers of mated pairs each year and numbers of adults that remain single because of skewed sex ratios. Three variants of the model are summarized below. Full equations can be found in electronic supplementary material, appendices A–C, and associated MATHEMATICA files and simulation files (in C) are deposited in the Dryad repository (doi:10.5061/dryad.4pn03).

(a) Mutual displays

In the primary model, both display and response occur in both sexes. Extra fecundity investment in response to the

display, f, is distributed among mated pairs of females (down the rows below) and males (across the columns) as

		Males			
		A_1B_1	A_1B_2	A_2B_1	A_2B_2
Females	A_1B_1	1	1	1	1
	A_1B_2	1	1	$1+f$	$1+f$
	A_2B_1	1	$1+f$	1	$1+f$
	A_2B_2	1	$1+f$	$1+f$	$1+2f+\rho f^2$

(2.1)

An important feature of this model is the parameter ρ, which describes a non-additive interaction in the fitness benefit of investment that may occur when both sexes respond to displays by their mates. If ρ is positive, then the benefits of investment by both partners are greater than twice the benefits of investment by one sex. If ρ is negative, then the benefits are less than the sum of the parents' contributions. A positive value for ρ is expected for many interactions between pairs. This is because, given that many more young are produced than survive to breed, small increments in nestling provisioning may give these young a great edge in competition. For example, experimental removals of one parent (i.e. approx. 50% reduction in parental investment) have often found that offspring fitness is decreased by much more than 50 per cent even before fledging; sometimes, offspring survival is reduced to zero [17,18].

After investment in offspring, males and females pay a survival cost for their display (selection coefficient s_m) and investment (s_f). Costs of display may also accrue through fecundity (s_{fec}), for example by attracting predators to the nest, or reducing foraging efficiency [19]. Analyses of fecundity costs are reported in the electronic supplementary material, appendix D. We assume that positive interactions between the investments by parents that increase fecundity ($\rho > 0$) do not increase the cost paid for investment. This assumption seems reasonable, because synergistic effects probably accrue directly through offspring fitness rather than by creating extra investment of the parents.

The costs of display and investment combine with a general, non-selective death rate (d) to determine mortality in adults. Death of one member of a pair creates an unmated individual, or single. Additional singles are created if a pair divorces, which occurs with probability ν. At the beginning of each breeding season, singles resulting from death and divorce, plus new recruits, pair at random, joining mated pairs that persisted intact from the previous year.

To analyse the model, we considered a wide range of initial conditions, and found that if the display and response are initially at a low frequency, then they generally do not increase unless the fecundity benefit from extra investment is very high. Most of the model results we present assume the frequency of the response allele is near-fixation, representing a hidden bias in the perceptual system of the receivers [20]. Such biases can arise for many reasons, including basic neurological wiring [20], tuning of the sensory system to ecological factors such as food [21] and the light environment [22]. A particularly relevant bias should arise from a parental focus on various offspring signals, which are used as provisioning cues [23]. These include mouthpart and feather colours in birds (e.g. figure 1*b*,*d*), as well as vocalizations. We concentrate on identifying those conditions under which a display trait introduced at low frequency becomes permanently established, as well as situations where it increases to near-fixation and is maintained at that frequency for some time before eventually being lost.

(b) Asymmetric displays

We modified the primary model to explore the evolution of investment when one sex, for simplicity considered to be the male, produces a costly display to which the other sex, i.e. the female, responds. In this case, extra fecundity investment, f, is distributed as

		males			
		A_1B_1	A_1B_2	A_2B_1	A_2B_2
females	A_1B_1	1	1	1	1
	A_1B_2	1	1	1	1
	A_2B_1	1	$1+f$	1	$1+f$
	A_2B_2	1	$1+f$	1	$1+f$

(2.2)

This model introduces added complexities with respect to the sex ratio, which often becomes skewed owing to differential mortality. Numbers of unmated males or females (the excess sex) are tracked in the model. We also consider a second variant of this model, which we term the *feedback* model. Here, both males and female display, and displaying males respond to female displays by increasing their display output, prompting a concomitant increase in the level of extra female investment. Such feedback loops have been demonstrated in experimental studies of mate choice [24]. The fecundity response in this model is represented as

		males			
		A_1B_1	A_1B_2	A_2B_1	A_2B_2
females	A_1B_1	1	1	1	1
	A_1B_2	1	1	1	1
	A_2B_1	1	$1+f$	1	$1+f$
	A_2B_2	1	$1+\gamma f$	1	$1+\gamma f$

(2.3)

The parameter γ represents how many times more a female will increase the boost to her investment if she receives an exaggerated signal from feedback between female and male displays, versus the original level of signal. In the feedback model, increases in display or investment scale the costs by β for increased display in males and γ for increased investment in females.

3. Results

(a) Mutual displays

The model of mutual displays includes the potential for an interaction between the investment by each of the sexes in their effects on offspring fitness. As noted in the methods, we assume the response allele to be initially at a high frequency and introduce the display at a low frequency. Two possible outcomes result: permanent fixation of the display and response alleles, or eventual loss of both. We consider each in turn.

When the fecundity benefit of investment is high relative to investment costs, the display and response can become permanently fixed. There are, however, two qualitatively distinct cases in which this occurs. In the first case (delineated by figure 2, area I), extra investment would evolve from a low frequency even if a display were not required to elicit such

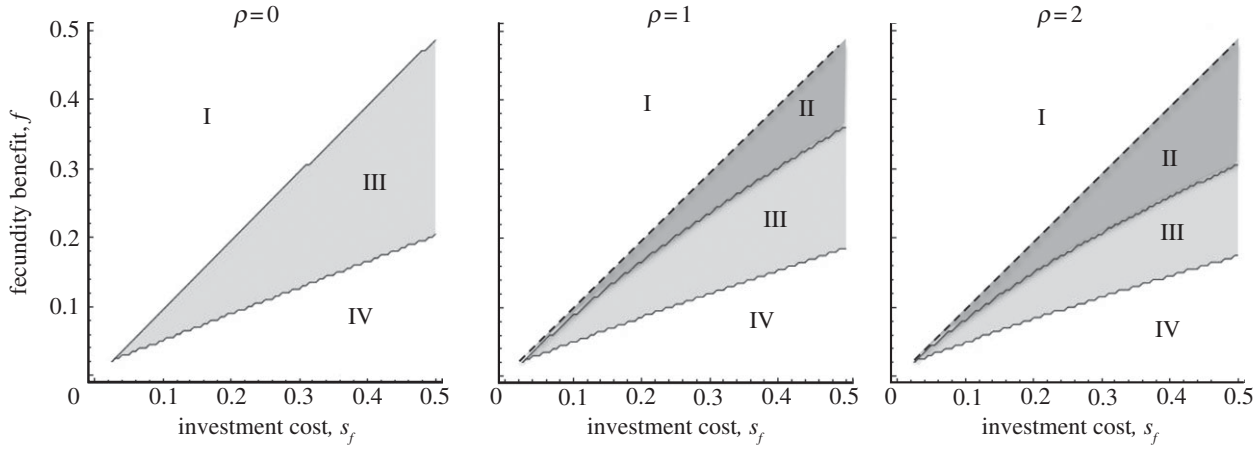

Figure 2. Conditions for permanent fixation of the display and response and transient evolution to a high frequency of the display in the symmetrical model. In area I, the display and response deterministically fix, but the starting conditions are such that increased investment (equivalent to the response) would evolve from low frequency if the display were not necessary for its expression. The dark grey area (area II) shows parameter space in which the interaction term ($\rho > 0$) leads to the permanent evolution of the display and response under conditions when extra investment would not evolve without being evoked by a display. The light grey area (area III) represents the parameter space for which, at some point during evolution of the display and response, the display is above a frequency cut-off of 0.95, whereas the response is below a cut-off of 0.05 (this outcome can last for thousands of years in some cases, as seen in figure 3). In area IV, the frequencies of the display and response are lost more rapidly and never cross the cut-offs specified earlier. For a very narrow range of parameters at the border of areas II and III, the response may remain polymorphic at equilibrium, whereas the display is fixed (see the electronic supplementary material). The response may also remain polymorphic at the bottom of the figure (area IV), when the display is lost before the response is lost. In this case, the response is neutral. Parameter values are s_m (selection against the display) = 0.01, d (intrinsic adult death rate excluding effects of selection) = 0.5, v (divorce rate) = 0.3, r (recombination rate) = 0.5, starting value of the response (A_2) = 0.99 and the starting value of the display (B_2) = 0.01.

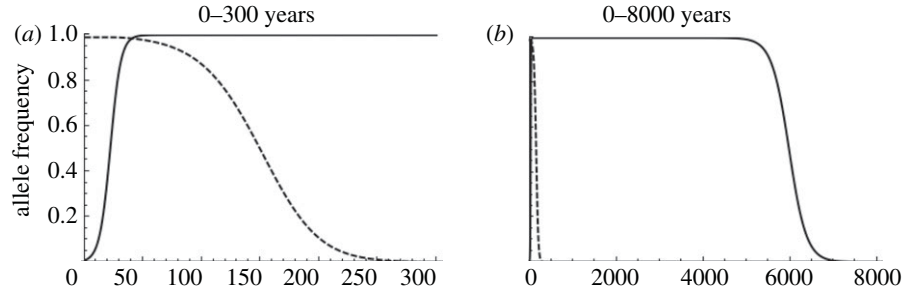

Figure 3. Evolution of display and response in the symmetrical model under conditions where the display increases transiently and there is no interaction between the fitness benefits from the partners ($\rho = 0$). Parameter values are as in figure 2, with f (fecundity benefit) = 0.5 and s_f (selection against fecundity investment) = 0.6. For clarity, the dynamics over the short term (first 300 years, (*a*)) and long term (8000 years, (*b*)) are plotted separately. Solid line denotes frequency of the display; dashed line denotes frequency of the response.

investment, as we confirmed with simulations (not shown). Hence, we consider that this is a region of parameter space with unlikely initial conditions and of little biological interest.

A second case is of more interest (figure 2, area II). This is a region of parameter space that appears only when the fitness benefits of investment interact positively ($\rho > 0$), and results in permanent fixation of both display and response when both would be lost without the interaction. The area of this region increases with the strength of the interaction (figure 2).

The evolutionary dynamics in this region are as follows. If most individuals are assumed to initially carry the response allele, as when there is a pre-existing bias, then the display when it first arises in one individual generally causes increased investment by the individual's partner. That increase in investment is detrimental and selected against. However, the displaying individual gains in fitness. Depending on the costs and benefits, the display may rise to high frequency before the response allele is appreciably reduced in frequency. The result is increased investment by a correspondingly large fraction of the population. At that time, many pairs contain individuals that both display and respond, and because of the positive interaction ($\rho > 0$), these pairs have higher productivity than pairs containing one or no displaying or responding individuals. Response alleles thus become favoured as well. The result is that the display and response increase to fixation, where they are permanently maintained.

In our models, we assumed responses were initially high, but we also varied the initial frequencies of the response allele, and found that it can be somewhat lower if the interaction is stronger (see the electronic supplementary material, figure D4). The key requirement is that the display, by increasing to high frequency, triggers the interactive benefits of extra investment by both members of a sufficient number of pairs. In this region of parameter space (figure 2, area II), simulations (not shown) indicate that investment alleles would not increase if introduced at a low frequency even if the display were initially fixed (mimicking the scenario where the display is not necessary to induce extra investment). Extra investment thus does not evolve except for the mechanism outlined here of pre-existing bias in response alleles, whose expression is triggered by an evolving display.

In other areas of the parameter space, display and response alleles are lost. We also separate this space into two regions (figure 2). First, if benefits of increased investment are relatively low and costs high, the response allele is strongly selected against as soon as the display is introduced (figure 2, area IV). Although the display may initially increase in frequency, both it and the response are rapidly lost from the population. Second, the display allele may rise to a high frequency, where it lingers before eventual loss (figure 2, area III). Figure 3 shows an example of the evolutionary dynamics of this case, in which the display takes a very long time to disappear after the response is lost (figure 3).

A negative interaction ($\rho < 0$), in which one sex interferes with the other, requires a higher benefit to cost ratio of female investment in order for the display and response to become fixed. Simulations demonstrate that this falls into the set of unlikely initial conditions, because the response would evolve even in the absence of the need for the display.

(b) Death and divorce

Because mutual displays seem especially prominent in relatively long-lived, pair-bonding, species, such as the great crested grebe (figure 1), we asked how variations in the death and divorce rate affect the probability of permanent fixation of displays.

In general, a high adult death rate (d) makes it relatively easy for displays to permanently invade (figure 4). When displays affect survival, and are hence incurred after young are fledged within a season, a high intrinsic death rate will lead to many individuals not paying these costs because they are dying anyway (this effect does not occur for fecundity costs, see electronic supplementary material, appendix D and figure D1). However, this positive effect of a high death rate on display establishment is misleading, because, as noted earlier, much of the parameter space over which this effect applies corresponds to the case where fecundity of a single individual is not optimized prior to introduction of the display. This case, above the solid line in figure 4, represents unlikely starting conditions.

The region of most interest lies below the solid line in figure 4, especially where a positive interaction leads to permanent fixation of the display trait in cases where it would be lost without the interaction. This is the area between the dashed ($\rho = 1$) or dotted ($\rho = 2$) lines and the continuous line ($\rho = 0$). As can be seen from figure 4, the parameter space inside this region is broader when the death rate d is low, i.e. a large number of individuals surviving from one season to the next allows the interaction term to have a large effect.

In contrast to death rates, we found that divorce rates made little difference to the outcome of the model (see the electronic supplementary material, appendix D), principally because they are unbiased with respect to the fitness benefits and costs.

(c) Asymmetric displays

The model where males stimulate females to invest more in their brood yields qualitatively similar dynamics to the model we have described earlier in the absence of an interaction in investment ($\rho = 0$), except that, because each type of selection falls only on one sex, rates of evolution are roughly halved. The chief difference between the asymmetric model and the model of mutual displays is that, because interactions are not possible, in the asymmetric model the male display and response cannot become fixed under realistic starting conditions. However, as in the model of mutual displays (figure 3), in some regions of parameter space, the display can increase to high frequency and remain there for a long time before it is eventually lost (see the electronic supplementary material, appendix D and figures D2 and D3).

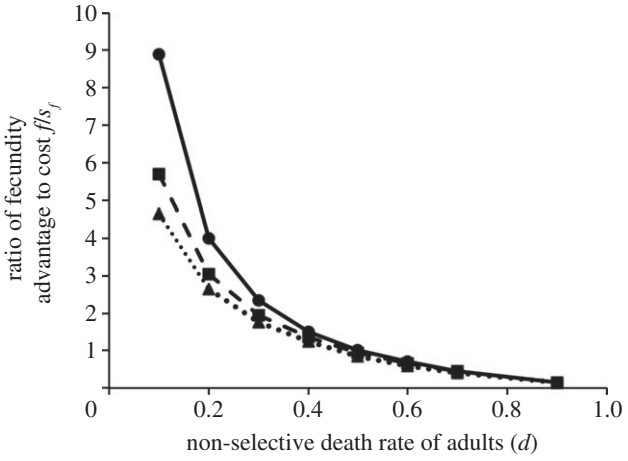

Figure 4. Effects of different levels of the interaction term. Parameter and starting values are as in figure 2 unless otherwise specified; death rate refers to the intrinsic adult death rate d, which is achieved in the absence of selection. Above each line, display and response are both fixed, whereas below each line, display and response are eventually both lost. Black solid (circles): ρ (interaction term) = 0, black dashed (squares): $\rho = 1.0$, black dotted (triangles): $\rho = 2.0$. The ratio on the y-axis was determined setting $s_f = 0.1$, and when $\rho > 0$ their position changes slightly for other values of s_f.

The feedback model, where the female stimulates the male to display more and thereby increase her own investment, gives very similar results to the general asymmetric model. Specifically, increases in the parameters for the effects of feedback on investment (γ) and display (β) have negligible effects on the outcome. First, the parameter γ affects both fecundity benefits and costs, so increases in γ have little effect on investment evolution. Second, the display parameter β alone has a trivial effect on the evolution of the display when the display parameter starts at low frequency; because the frequency of pairs in which both the males and females display is low, excess costs are rarely paid.

4. Discussion

Many displays in nature occur between individuals with established pair bonds. The primary function of these displays has been difficult to explain, with sexual selection thought unlikely to be the sole, or even major, cause [6,25]. Here, we have considered that such displays elevate parental investment rather than attract mates. We show that exaggerated mutual displays can be permanently established if the benefits of increased investment interact positively, by a mechanism of pre-existing bias of the investment response. The actual magnitude of the interaction required for establishment of the mutual display depends on multiple factors, including the baseline death rate and the costs of display and investment (figures 2 and 4). In its substance, the criterion for the deterministic maintenance of mutual displays corresponds with results from models of cooperation termed 'by-product mutualisms' (reviewed in Sachs *et al.* [26]), whereby an individual directly and immediately increases its own fitness by cooperating.

It is easy to imagine scenarios where contributions from both members of the pair increase fitness beyond twice that expected from investment by a single individual. Indeed, the commonest explanation for the presence of monogamy itself is that two parents can successfully raise more than twice the number of surviving offspring than a single parent can [27], as has been demonstrated by removal experiments [17]. In our models, we find that low adult mortality results in the largest parameter space over which interactions make displays most likely to evolve (figure 4). In accordance with this finding, it is in relatively long-lived species where such displays appear common. For example, the two species illustrated in figure 1 with the most obvious mutual displays are the great crested grebe, with an annual adult mortality rate estimated at about 0.25 [28] and the yellow-legged gull (*Larus michahellis*), with an estimated adult mortality of less than 0.15 [29]. Thus, evolution by mutual mate stimulation appears particularly likely in those long-lived, essentially monomorphic, pair-bonding species, which are exactly those species where sexual selection appears to be particularly unlikely [6].

We also considered a scenario where investment by both parents leads to a negative interaction, as could result from sexual conflict ([30]; $\rho < 0$ in our model). We find that in this case displays and responses do not evolve in a realistic area of the parameter space, suggesting that this particular form of conflict will prevent display evolution by the mechanism of inducing investment.

In addition to the permanent fixation of displays, which happens when interactions are strong, there is a large region of parameter space over which the display can persist for many generations before eventually being lost (figures 2 and 3). This region is of interest, for it occurs both in mutual displays without an interaction, and in asymmetric displays in which one sex stimulates investment by the other (see the electronic supplementary material, figures D2 and D3). In our models of this process, displays are always eventually lost, but logic suggests that permanent maintenance of the display could result from evolution at other loci affecting clutch size. Consider an example from the asymmetric scenario, where a novel male display induces females to overinvest in clutch size and hence the female response is selected against. Consequently, *any* alleles reducing clutch size, including those at loci other than the response locus, are favoured. Indeed, loci affecting clutch size are known to be heritable and readily respond to selection [31], and hence may generally evolve rapidly. By contrast, even though the response locus is selected against in the context of investment, our models may overestimate its rate of loss; if, as we suggest, the response originates from a pre-existing bias, it may be selectively maintained in other contexts (e.g. females that respond to orange males may be tuned to orange foods [21]). The result of evolution of clutch size at loci other than the response locus should be adaptive maintenance of both the display and the response, because loss of either would result in females producing clutch sizes that are too small. Co-evolution may be so strong that some male displays are required for females to even ovulate [32]. This verbal argument is similar to that made by Holland & Rice [33] in the context of sexual selection.

Previous theory on display evolution through parental investment has assumed that displays are correlated with mate quality, and that an individual's increased investment when paired with an attractive mate is an adaptive strategy to improve offspring quality. This has become known as the 'differential allocation hypothesis' [9,16,34]. Our result of permanent evolution of display and investment response in the symmetrical model, as well as the earlier-mentioned verbal argument regarding transient cases, suggest that experimental manipulations of traits that induce increased investment may simply be manifestations of both the display and response being required to produce the clutch of optimal size, rather than any higher-order differential investment strategies. Differential allocation models have been extended to consider how males and females may adaptively adjust investment into their brood depending on the contributions of the other when there is sexual conflict (e.g. 'negotiation' over care; [35]). It would be of interest to further extend these models by adding the possibility that the behaviour of one sex is essential stimulation to the other.

Mate stimulation provides one explanation for the presence of socially selected traits in females. Other explanations for the evolution of female displays have emphasized sexual selection by male mate choice [36] and their use in threat situations [5,37,38], but these are in themselves unable to account for those displays between the sexes that arise post-pairing [5,25,38]. Plausibly, mate stimulation, threat and sexual selection by male choice all operate through the same sensory biases, and act synergistically to drive the evolution of socially selected traits in females [10,11]. In the great crested grebe, both males and females gain showy traits in the breeding season, but the male becomes more showy, suggesting a combination of symmetric and asymmetric factors are involved, and these may include mate choice as well as investment.

In the model developed here divorce makes little difference to evolutionary outcomes (see the electronic supplementary material, appendix D), but this is not likely to hold if the model is modified to include positive effects of familiarity on reproductive success [2]. Hence, we have not directly addressed those factors that lead to the maintenance of the pair bond. Instead, we have shown that once pair bonds are established, each sex will commonly evolve in response to the 'environment' imposed by the other. Our results indicate that cooperation and attendant displays are likely to regularly evolve in the consequence of stimulation by one member of the pair to increase investment by the other.

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